

Article

Size-dependent locomotory performance creates a behaviorally mediated prey size refuge in the marine snail *Olivella semistriata*: a study in the natural habitat

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Abstract

The effects of the variability of individual prey locomotory performance on the vulnerability to predation are poorly understood, partly because individual performance is difficult to determine in natural habitats. To gain insights into the role(s) of individual variation in predatory relationships, we study a convenient model system, the neotropical sandy beach gastropod *Olivella semistriata* and its main predator, the carnivorous snail *Agaronia propatula*. The largest size class of *O. semistriata* is known to be missing from *A. propatula*'s spectrum of subdued prey, although the predator regularly captures much larger individuals of other taxa. To resolve this conundrum, we analyzed predation attempts in the wild. While *A. propatula* attacked *O. semistriata* of all sizes, large prey specimens usually escaped by 'sculling', an accelerated, stepping mode of locomotion. *Olivella semistriata* performed sculling locomotion regardless of size, but sculling velocities determined in the natural environment increased strongly with size. Thus, growth in size as such does not establish a prey size refuge in which *O. semistriata* is safe from predation. Rather, a behaviorally mediated size refuge is created through the size-dependence of sculling performance. Taken together, this work presents a rare quantitative characterization in the natural habitat of the causal sequence from the size-dependence of individual performance, to the prey size-dependent outcome of predation attempts, to the size bias in the predator's prey spectrum.

Key words: Escape response, Prey size refuge, Locomotory performance, Predator–prey size ratio, *Olivella semistriata*, *Agaronia propatula*

Locomotory performance, the efficiency of locomotion in terms of acceleration, speed, maneuvering abilities, and endurance, relates to survival and thus to fitness in mobile prey species (Webb 1986). Unfortunately, the practical determination of the role of locomotory performance in predator–prey relationships is complicated by several factors. First, locomotion performed in controlled settings does not necessarily reflect locomotory performance in the wild (Irschick

and Garland 2001). Similarly, prey escape responses triggered by artificial stimuli in experiments are not necessarily valid models for prey behavior under attack by a real predator that may show variable behavior itself. Therefore, behavioral studies in natural habitats are essential for understanding the ecological and evolutionary significance of prey locomotory capabilities in the context of escape responses (Moore and Biewener 2015). Second, behavior and

performance in a given situation may differ individually, be it because individuals exhibit different ‘personalities’ (Wolf and Weissing 2012), or because individual capabilities change in the course of ontogenetic development (De Roos and Persson 2013). As a result, averaging performance over a population or species is likely to produce misleading results. Consequently, investigations into the role(s) of locomotory performance should focus on individual interactions between predator and prey, especially if individual variability must be suspected to be of a systematic rather than stochastic nature (Nakazawa 2017).

Among classical investigations into predator–prey interactions that drove the development of ecological theory, studies of intertidal benthic invertebrate communities were particularly influential (Robles and Desharnais 2002). Marine gastropods, for example, respond to invertebrate predators with a variety of defensive behaviors including flight (Ansell 1969), and several population- and community-level effects of gastropod defense responses have been characterized (Fishlyn and Phillips 1980; Hadlock 1980; Garrity and Levings 1981). Still, the ecological relevance of numerous apparent flight responses described in marine gastropods has remained unclear. Gastropod flight velocities were rarely quantified and the dependence of locomotory performance on individual body size seems to have been determined in not more than a single study. Schmitt (1981) found positive correlations between size and speed of locomotion in three of the four gastropod species he tested; all tests were conducted in the laboratory. Whether these correlations affected predator–prey interactions in the natural habitats has been left unexplored.

The carnivorous snail, *Agaronia propatula* Conrad 1849 (Olividae, Caenogastropoda), inhabits sandy beaches of the Central American west coast (Keen 1971). Its predation and feeding behavior, which resembles that reported from other large olivids (Kantor and Tursch 2001; Kantor et al. 2017), has been described in detail (Rupert and Peters 2011; Cyrus et al. 2012, 2015). The animals hunt actively. Prey is grasped with the anterior foot and then secured by the posterior foot or metapodium, which bends ventrally to form a spherical pouch that encloses the prey item (compare Supplementary Video S4). The highly extensible proboscis carrying the mouth opening at its end is inserted into the metapodial pouch for feeding. Analyses of metapodial pouch contents in *A. propatula* revealed the suspension-feeding snail, *Olivella semistriata* Gray 1839, of the same family as the dominant prey (Robinson and Peters 2018). Intriguingly, large *O. semistriata* (maximal shell length is about 2.1 cm; Troost et al. 2012) were missing from the prey spectrum of *A. propatula*, suggesting that *O. semistriata* can reach a size refuge from predation. Prey size refugia (Chase 1999) are frequently interpreted as resulting from gape-limited predation, where the size of a predator’s gape or capture apparatus defines maximum prey size (Urban 2007; for a case study involving marine gastropods, see Boulding et al. 2016). While large olivid predators including *A. propatula* are not gape-limited in the literal sense as they do not swallow their prey whole, the dimensions of their metapodial pouches probably set limits to prey size. Such limits, however, cannot explain the observed absence of large *O. semistriata* from the prey spectrum of *A. propatula*, as even the largest *O. semistriata* are much smaller than some of the bivalves, crustaceans, and con-specifics that were found in the predators’ metapodial pouches (Robinson and Peters 2018). Thus, the mechanism behind the size bias against large *O. semistriata* is unlikely to be purely mechanical, and may include behavioral factors such as locomotory performance.

When disturbed, crawling *O. semistriata* temporarily switch to an accelerated, stepping locomotion mode (Seilacher 1959) that is reminiscent of a person sculling a boat (Supplementary Video S2). We hypothesized that flight by “sculling” might help *O. semistriata* to avoid predation by *A. propatula* in a size-dependent manner, and tested the idea in the natural habitat.

Materials and Methods

Notes on 57 naturally occurring attacks by *Agaronia propatula* on *Olivella semistriata* were collected during field trips (2011–2014 and 2017, but not during the strong El Niño 2015–2016) to Playa Grande, Costa Rica (10°20′N, 85°51′W). Twenty observations (35%) were made in the dry season (December–April), 23 (40%) in the rainy season (late May–October), and 14 (25%) during the transition in early May (Supplementary Table S1). Details were recorded immediately at the location in writing; in a few cases, videos of the attacks were recorded using digital cameras. An interaction between *A. propatula* and *O. semistriata* was classified as an “attack” if the predator executed at least one strike with its anterior foot at the prey (Figure 1A; compare Cyrus et al. 2012). Attacks

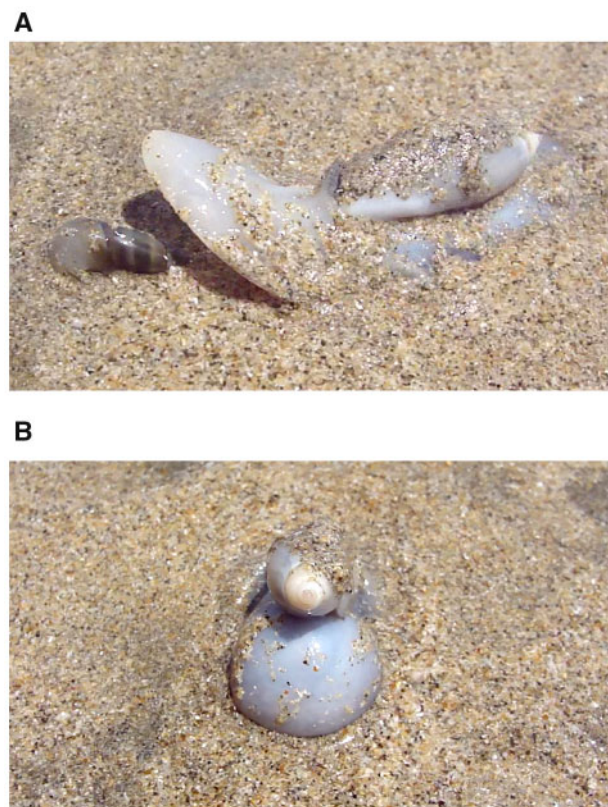


Figure 1. Stages in the predatory attacking behavior of *Agaronia propatula* critical to our analysis of field observations. (A) *Agaronia propatula* initiates an attack on *Olivella semistriata* by executing a fast strike at its victim with the anterior part of the foot. Only when such a strike was executed the interaction was counted as a predatory attack. (B) After successful completion of the attack, the prey is enclosed by the posterior foot, which forms the spherical metapodial pouch, and the predator burrows into the sediment to consume its prey. Only when *A. propatula* had started to burrow with the prey firmly enclosed in the pouch, the attack was recorded as successful. The shell lengths of the animals shown are 31.1 mm (*A. propatula*) and 17.2 mm (*O. semistriata*).

were classified as “successful” when *A. propatula* had stored the prey in the metapodial pouch and started to burrow into the sediment (Figure 1B). After each attack, predator and prey shell lengths (siphonal notch to apex) were measured to the nearest 0.1 mm with calipers or on digital photographs (taken with various standard cameras, Panasonic DMC-FZ30; Sony DSC-H20; Nikon Coolpix AW130) of the animals next to a ruler (ImageJ; <https://imagej.nih.gov/ij>). The original data is available as Supplementary Table S1.

To establish trajectories of linearly moving *O. semistriata*, digital cameras (Sony DSC-H20) on small tripods were positioned with the sightline perpendicular to the anticipated path. Sculling locomotion was induced by gently touching the shell apex of a crawling animal (Supplementary Video S2). Videos were taken at 30 frames per second and 1280 × 720 pixel resolution, and the position of the shell apex was determined on each frame (ImageJ). Loess smoothing was applied to these data to provide continuous trajectories, and numerical derivation yielded velocity functions (TableCurve 2D; <https://sys.tatsoftware.com>).

Dependences of the distribution of successful and unsuccessful attacks on predator size, prey size, and the size ratio (Figure 2B–D) were analyzed by Mann–Whitney U-tests online at <http://www.vas.sarstats.net>. The correlation between body size (shell length) and the velocity of the escape response (Figure 4C) was described by the geometric mean functional relationship (GMFR; Draper and Smith 1998). The strength of the correlation was quantified by the coefficient of determination (r^2) based on Pearson’s correlation coefficient, r .

Results

We documented 57 attacks of *A. propatula* on *O. semistriata* in the wild, of which two-thirds were successful (Table 1). In 48 cases, *O. semistriata* initiated sculling and escaped in 18 of these attempts (Table 1). Escape attempts by sculling generally succeeded if *O. semistriata* propelled itself beyond the immediate reach of the attacker within the first 2 s of the initial attack (compare Supplementary Videos S3 and S4). In the remaining nine attacks, no sculling was attempted, mostly because the initial strike was immediately successful and/or the victim was partly embedded in the sediment. In one of these nine attacks, the victim escaped by crawling (Table 1).

The outcome of the observed attacks depended on the size relationship between *A. propatula* and *O. semistriata* (Figure 2A). All attacks were successful if the shell length of *O. semistriata* was <11.8 cm; attacks were always unsuccessful, with one exception, if the shell length was >18.2 cm (Figure 2A; compare Supplementary Table S1). Unsuccessful predation attempts were associated with low predator–prey size ratios (Figure 2B). Both prey and predator size contributed to the effect, but the influence of prey size appeared stronger (Figure 2C and D).

Olivella semistriata usually switched from crawling to sculling locomotion when it was touched posteriorly by an *A. propatula* (Supplementary Videos S3, S4). This stimulus could be mimicked by

gently touching the shell apex of a crawling *O. semistriata* (Supplementary Video S2), which facilitated quantitative analysis. Sculling locomotion consisted of a series of steps that covered about half the animal’s shell length each within 0.5–0.9 s. Sculling was several times faster than regular crawling, but was never sustained for more than 4–5 s (see representative analysis in Figure 3). When sculling, bigger animals covered longer distances per unit time than smaller ones (Figure 4A). In contrast, trajectories of all snails were similar when distances were expressed as shell lengths (Figure 4B). Evidently, sculling velocity was a function of body size.

To determine the dependence of sculling velocity on size more precisely, we induced sculling in crawling animals of different sizes that otherwise were undisturbed in their habitat. Because the initial response phase seemed crucial for escape success, we focused on velocities averaged over the first 2 s of sculling locomotion. Averaged initial velocity and shell length were correlated ($r^2 = 0.58$, $n = 125$); velocity increased by about 0.12 cm/s per one-mm increase in shell length (Figure 4C). There was no such correlation when velocity was expressed relative to body size, i.e., as shell length per second (Figure 4D).

Discussion

A key finding emerging from the analysis of predation attempts that occurred in the natural habitat was that large *O. semistriata* were in fact attacked by *A. propatula* but mostly escaped (Figure 2). This result provided a sufficient explanation for the fact that large *O. semistriata* had not been found among the prey cached in metapodial pouches of *A. propatula* (Robinson and Peters 2018). Consequently, a prey preference executed by the predator is not required to account for the size-bias in the prey spectrum.

As a rule, successfully escaping *O. semistriata* applied sculling locomotion (Table 1). Sculling velocity averaged over the first 2 s of the flight response rose 6-fold from the smallest to the largest animals tested (Figure 4C). At this time, we lack information about the size-dependence of crawling speed in *A. propatula*, but peak velocities around 0.9 cm/s have been recorded (Cyrus et al. 2012). This astonishing value is about twice the speed reported for other large predatory olivids, arguably the fastest gastropods (Tursch and Greifeneder 2001). If we accept the simplifying premise that hunting *A. propatula* regularly reach such velocities regardless of their own size, and further assume that the success of flight depends on *O. semistriata*’s initial velocity after the induction of sculling, we will be able to draw two inferences from Figure 4C. First, *O. semistriata* of 12 mm shell length or more will have a significant chance to escape a charging *A. propatula*. Second, *O. semistriata* of over 17 mm almost always will outrun their attacker. These predictions, though based on simplifying assumptions, are in excellent agreement with our observations of successful escapes in the field (Figure 2A). There are additional relevant factors, as indicated by the observation of successful predation attempts in which no sculling locomotion was initiated (Table 1). Nonetheless, the size-dependence of sculling

Table 1. Attacks of *Agaronia propatula* on *Olivella semistriata* observed in the wild

Prey behavior	Attack successful	Attack unsuccessful	Row total
Sculling locomotion initiated	30 (53%)	18 (31%)	48 (84%)
No sculling locomotion initiated	8 (14%)	1 (2%)	9 (16%)
Column total	38 (67%)	19 (33%)	57 (100%)

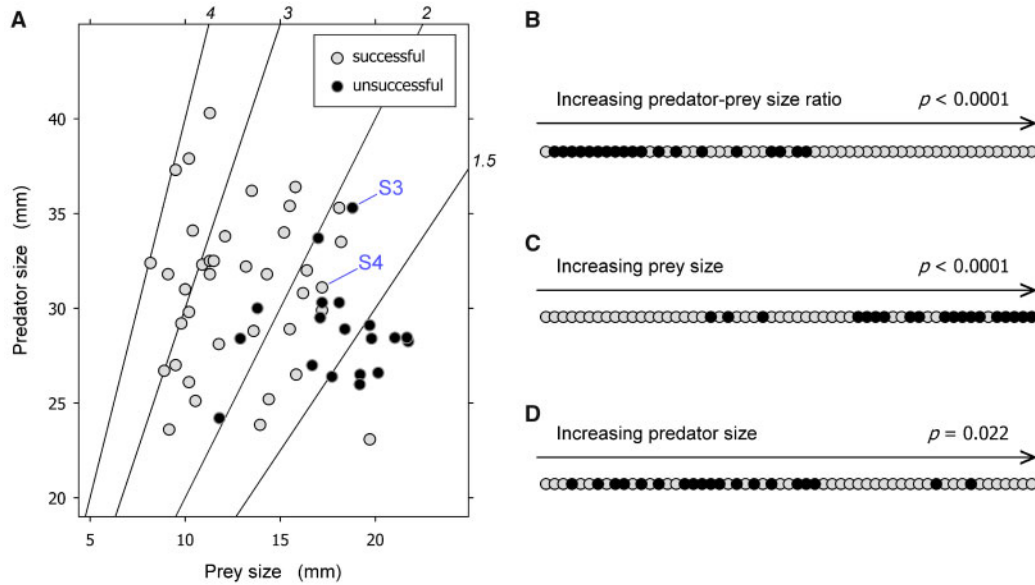


Figure 2. Attacks of *Agaronia propatula* on *Olivella semistriata* recorded in the wild. (A) Size relations between prey and predators, given as shell lengths for the observed 38 successful and 19 unsuccessful attacks. Examples presented as [Supplementary Videos S3 and S4](#) are marked. Straight lines mark the size ratios 1.5, 2, 3, and 4 (indicated at upper ends of lines). (B, C, D) The same attacks as in (A) ranked with increasing predator-prey size ratio, prey size, and predator size, respectively. P , probabilities for obtaining distributions at least as strongly skewed as the observed ones in the absence of any real size-dependence (Mann-Whitney U-test, two-tailed).

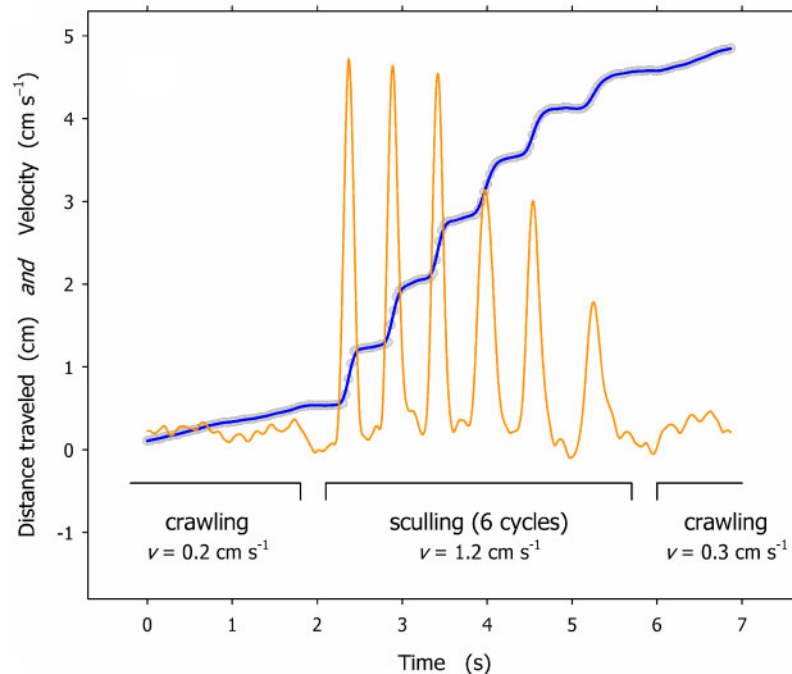


Figure 3. Locomotion kinematics of *Olivella semistriata*. The movement of a representative animal of 15.6 mm shell length is shown; phases of regular crawling and sculling locomotion with average velocities are highlighted. Gray circles, position of the shell apex (from a video taken at 30 frames per second); blue line, trajectory (Loess smoothing applied to data); orange line, velocity (derivative of trajectory).

velocity is sufficient to explain why the observed attacks of *A. propatula* on large *O. semistriata* were largely unsuccessful.

Quantitative assessments of individual flight capabilities in natural environments (such as our tests summarized in [Figure 4](#)) are complicated when the animals are forced to trade speed for maneuverability by the structural complexity of three-dimensional terrains

([Wheatley et al. 2015](#)), or by the need to outmaneuver predators that cannot be outrun ([Clemente and Wilson 2015](#)). These problems are of limited relevance with our study species, for two reasons. First, structural simplicity is a character of our study species' habitat. Both species burrow into the sediment to rest ([Seilacher 1959](#), [Troost et al. 2012](#)), but their predator-prey interactions generally

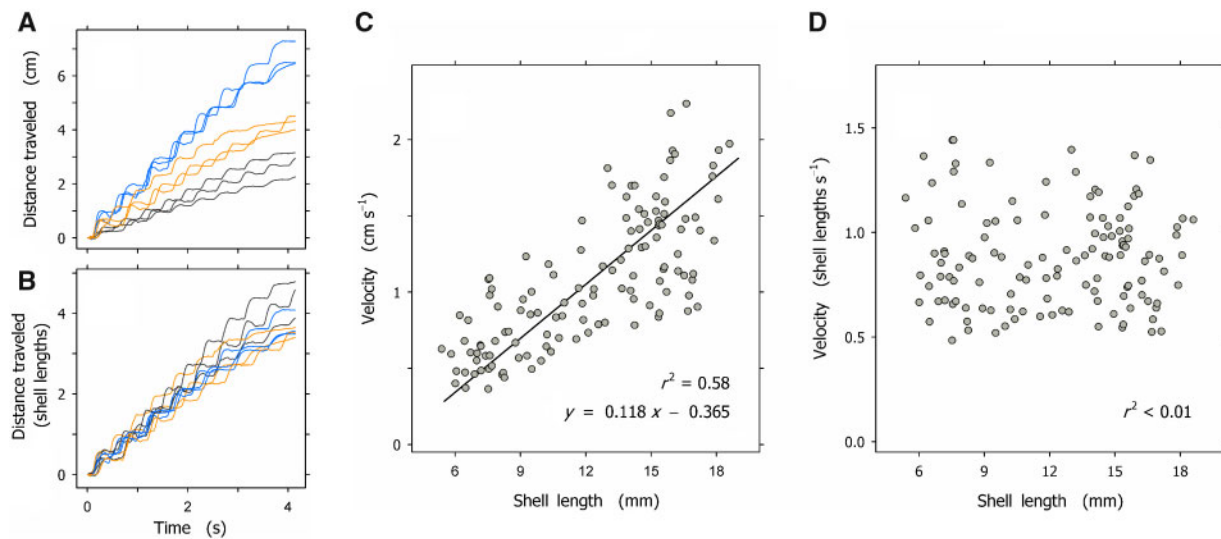


Figure 4. Sculling velocity depends on size in *Olivella semistriata*. (A, B) Trajectories of nine representative animals of three size classes (large, blue: 18.6, 18.1, 17.8 mm shell length; medium, orange: 12.8, 11.9, 11.8 mm; small, gray: 6.6, 6.4, 5.8 mm), expressed as absolute distances (cm; A) and as relative distances (shell lengths; B). The dependence of velocity on body size during the first 2 s of the response (dark background) was further analysed in a larger sample. (C) Average velocities over the first 2 s after initiation of sculling locomotion, plotted against shell length for 125 individuals. The coefficient of determination (r^2) and the geometric mean functional relationship and its equation are shown. (D) As (C), with velocities expressed as shell lengths per second.

occur on the surface of the beach sediment, essentially a two-dimensional stage. Second, speed and maneuverability certainly are antagonistic factors in animals moving at many body lengths per second (e.g. quadrupeds, fishes, ants; Wilson et al. 2015). In contrast, snails and other small animals moving at fractions of their body lengths per second certainly are too slow, given body masses of a few grams at most, for inertia effects to impair maneuvering abilities.

Prey may grow into size refuges when it becomes too large to be handled by predators (Chase 1999; Urban 2007; Taborsky et al. 2018). For individuals in prey size refuges, active flight behavior might become dispensable. For instance, immature individuals of several aquatic gastropod species execute flight responses when they sense certain predators, but abandon this responsiveness after having reached sizes that exclude them as potential prey of these predators (Hoffman and Weldon 1978; Branch 1979; Alexander and Covich 1991). In contrast, *O. semistriata* of all sizes attempt to flee by sculling when attacked by *A. propatula*, but larger individuals exhibit superior locomotory performances (Figure 4C) and thus have an increased chance of escaping successfully (Figure 2). We conclude that it is not size as such that physically prevents predation in *O. semistriata*. Instead, a parameter correlated with size, sculling velocity, creates a behaviorally mediated size refuge. *Olivella semistriata* gradually moves into this size refuge as it grows from about 12 mm to 17 mm shell length.

If a prey species shows a pronounced positive correlation between body size and locomotory performance, and if its susceptibility to predation decreases with increasing locomotory performance, predation must be expected to select for faster growth and larger maximum size in this species. Other selection factors, however, may override the effects of predation pressure, and this seems to apply to *O. semistriata*. The species reaches highly variable sizes at different locations, as indicated by dwarfish populations originally described as a separate taxon, *O. attenuata* Reeve 1851 (Troost et al. 2012). Maximum sizes of *O. semistriata* at different Costa-Rican locations did not correlate with local densities of *A. propatula* and sometimes remained below 12 mm shell length (Troost et al. 2012), the

estimated lower limit of the transition into the size refuge (Figure 2A). Evidently, currently unknown factors other than predation by *A. propatula* exert influence on growth and development in *O. semistriata*. In this context, we note that a positive correlation of escape success with body size cannot drive selection for larger maximum size in prey that grows into a size refuge before it reaches its size maximum. However, selection for faster growth into the refuge still must be expected. Quantitative analyses of the development of *O. semistriata* in different populations will clarify whether the species responds to predation pressure by increased growth rates that enable it to reach the size refuge more quickly.

The link(s) between locomotory performance and prey fitness remain obscure (Wilson et al. 2015), mainly because of difficulties in measuring performance in its natural ecological context (Irschick and Garland 2001; Irschick 2003) and insufficient information on the effects of individual variability (Nakazawa 2017). We addressed both problems using a molluscan predator-prey relationship, which provided a useful model system due to the accessibility and simple structure of the habitat. The present study may be the first to quantitatively characterize the causal chain leading from the size-dependence of individual performance (Figure 4), over the success rate of actual predation attempts (Figure 2), to the size bias in the predator's prey spectrum (Robinson and Peters 2018), based entirely on information collected in the natural habitat.

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Supplementary material

Supplementary material can be found at <https://academic.oup.com/cz>

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